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Source: The American Midland Naturalist, 171(2):328-339. 2014.

Published By: University of Notre Dame

DOI: <http://dx.doi.org/10.1674/0003-0031-171.2.328>

URL: <http://www.bioone.org/doi/full/10.1674/0003-0031-171.2.328>

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# The Population Ecology of the Threatened Inflated Heelsplitter, *Potamilus inflatus*, in the Amite River, Louisiana

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**ABSTRACT.**—We quantitatively sampled the threatened Inflated Heelsplitter (*Potamilus inflatus*) in the Amite River, Louisiana, U.S.A., and sectioned shells to study its life history, as well as electrofishing the river to determine the relative abundance of its host fish. Inflated Heelsplitters are currently limited to a 40 km stretch of the Amite River, east of Baton Rouge, although they are also found in two rivers in northwest Alabama. Densities averaged  $0.1\text{ m}^{-2}$ , with an aggregated dispersion pattern, making them the sixth most abundant species out of 15 species found in quantitative samples. Inflated Heelsplitters mature after 1 y, live for 8 y, and have a rapid growth rate ( $K = 0.69/\text{y}$ ). The average life span of eight other mussels in the Amite River is 24 y, and average age at maturity is 3.6 y. Sexual dimorphism may occur in Inflated Heelsplitters as it does in the related Bluefers (*Potamilus purpuratus*), with males reaching larger sizes. Inflated Heelsplitters have an opportunistic life history strategy (Haag, 2012), which may be well adapted to flashy rivers and low population densities. It is however a long term brooder, which has been linked to higher chances of extinction (Vaughn, 2012). The Freshwater Drum (*Aplodinotus grunniens*), the fish host of the Inflated Heelsplitter, was the 17th most abundant out of 44 fish species sampled in the Amite River. Its relatively rare host fish, anthropomorphic disturbances from upstream gravel mining, or increased urbanization of the watershed may be important in explaining the threatened status of the Inflated Heelsplitter.

## INTRODUCTION

Unionid Mussels are the most endangered freshwater organisms, with roughly three quarters of the species in the United States considered in peril (Williams *et al.*, 1993; Strayer, 2008). Risks include habitat loss or alteration, riparian development, disruption of host fish dispersal by impoundments, pollution, and invasive species (Bogan, 1993; Williams *et al.*, 1993; Neves *et al.*, 1997). Unionid mussels are particularly susceptible to habitat disturbances because of relatively long life cycles, poor dispersal, sedentary adults, and a complex life cycle (Vaughn and Taylor, 2000). Schwalb *et al.* (2011) suggested common mussels tend to be large, use large host fish that disperse long distances, or use multiple host fish. However, Vaughn (2012) argued that mussels with attraction displays had greater colonization rates, while species reproducing less frequently or relying on fish like gar or Freshwater Drum that dispersed long distances, had higher extinction rates. She considered impoundments as likely to interfere with the movements of these more mobile fish.

The Inflated Heelsplitter, *Potamilus inflatus* (Lea, 1831), historically occurred in the Amite, Tangipahoa, and Pearl Rivers in south-eastern Louisiana and the Tombigbee and Black Warrior Rivers in Alabama (Stewart, 1993). However, in Louisiana, it is now restricted to a 40 km stretch of the Amite River from Spiller's Creek to Port Vincent (Hartfield, 1993; Brown and Curole, 1997; USFWS, 2009) and was listed as threatened in 1991 (USFWS, 1991). Inflated Heelsplitters are found in soft substrates in low or moderate flows and have a thin symphynote (winged) shell with increased surface area that evidently decreases their chances of burial in soft sediments (Watters, 1994; Haag, 2012). The Amite River population is under the dual threats of gravel mining in the northern portion of its range, which results

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in channel widening, braided flow, and bank destabilization that lead to higher stranding rates of mussels (Hartfield, 1993; Brown and Curole, 1997), and increased urbanization of the watershed in the lower portion of its range (Brown *et al.*, 2010). Although considered conspecific, as much genetic variation occurs between the Louisiana and Alabama populations of *Potamilius inflatus* as occurs between other *Potamilius* species (Roe and Lydeard, 1998). *Leptodea fragilis* is considered, based on molecular data, to be its sister clade. The Inflated Heelsplitter is considered a long term brooder, holding embryos for almost a year (Roe *et al.*, 1997). As some evidence suggests, males reach larger sizes than females (Hartfield and Garner, 1995; Williams *et al.*, 2008). The host fish is the Freshwater Drum, *Aplodinotus grunniens* (Roe *et al.*, 1997). Haag (2012) considered *Potamilius* spp. and *Leptodea* to be “riverine lentic microhabitat specialists” that coexist with other mussels by using littoral habitats with slower flows and softer sediments. *Potamilius* spp. are larval broadcasters and are considered to have an “opportunistic” life history strategy involving rapid growth, early maturity, high fecundity, and short life spans (Haag, 2012).

In this paper, we are interested in the following hypotheses: the threatened Inflated Heelsplitter, compared to other common unionids in the Amite River, (1) has lower densities, (2) has as predicted a more opportunistic life history, and (3) has a relatively rare host fish and thus reduced chances of dispersal. We estimated densities of Inflated Heelsplitters using quantitative sampling and compared them to densities of other common unionids. We also estimated dispersion patterns, to determine if the threatened species had a more patchy distribution. We used annual growth rings laid down in the shell to estimate the growth rate, approximate age at maturity, and life cycle length and compared these traits to the related *Potamilius purpuratus* (Bluefer) and *Leptodea fragilis* (Fragile Paper Shell). We also used the growth curves to determine the age distribution of Inflated Heelsplitters in the Amite River. To determine the relative abundance of its host fish, we electro-fished sections of the Amite River where Inflated Heelsplitters are found. We also used these data to see if there is any clear correlation between the abundance of common unionids in the Amite River and the abundance of their known host fish.

## METHODS

### HABITAT DESCRIPTION

The Amite River flows south from headwaters near Jackson, Mississippi into Louisiana, where it drains into Lake Maurepas. It is a warm water, low gradient coastal stream formed by glacial melting in the Cretaceous (Folley, 1992). The upper reaches in Louisiana are characterized by faster flows with sand or gravel substrata, while the lower reaches closer to Lake Maurepas are meandering, bayou-like rivers with slower flow, silt sediments overlaying sand, and extensive riparian wetlands. The wet season, with 69% of the annual discharge, occurs in Winter and Spring, and Summer and Fall are lower discharge periods, although urbanization of the watershed near Baton Rouge has increased discharges by 55% during the last 40 y (Xu and Wu, 2006; Wu and Xu, 2007). Temperatures average 20 C and vary from a low of 12 to a high of 32 C, with dissolved oxygen concentrations seldom below 70% saturation. The pH averages 6.2, conductivity ranges from 180–220  $\mu\text{Scm}^{-1}$ , hardness averages 13  $\text{mgL}^{-1}$ , and turbidity is approximately 50 JTU (Folley, 1992). The central region of the watershed in Louisiana, roughly from the Louisiana Highway 10 bridge to Spiller’s Creek, has undergone extensive gravel mining, beginning in the 1950s and peaking in the 1980s (Mossa and McClean, 1997).

### QUANTITATIVE SAMPLING

To estimate the density and dispersion patterns of Inflated Heelsplitters and other unionid mussels in the Amite River, we used quantitative quadrat sampling modified after

Strayer and Smith (2003). Thirteen sites (from 30°34'0.19"N, 90°58'27.6"W to 30°20'53.2"N, 90°54'02.5"W) were selected along the stretch of the Amite River known to contain Inflated Heelsplitters (Brown and Curole, 1997; Brown *et al.*, 2010) and were sampled during May–Aug., 2011. Sampling sites were selected to be 1–2 km apart to be independent, and an effort was made to select all major habitat types (sand bars, protected littoral areas with silt sediments, muddy banks, *etc.*). At each site, we selected five random starting points in the littoral zone of the river. Shallow littoral areas (*e.g.*, less than 2 m depth) were chosen because mussel densities are higher in these more protected habitats than in the main thalweg (Brown and Curole, 1997; Brown and Banks, 2001). At each of five starting points, we laid out a transect parallel to the shoreline that was 10 m long and 1 m wide. The transect was marked on either side with PVC poles every meter with a chain stretched on the substrate between the poles. This allowed divers with SCUBA gear to remain within the transect. One diver removed all adult mussels along the whole transect and identified them. A second diver used a Keene Inc. powered suction dredge to excavate every other square meter for juvenile mussels, down to a depth of 15 cm. All mussels were pooled over the whole transect (the sampling unit) and total mussel densities were converted to a square meter basis. We compared mussel densities among unionid species using a one-way analysis of variance (SAS Inc., 2005), with Tukey's *a posteriori* tests used to compare individual densities among species. We estimated dispersion patterns of each species using Morisita's index. Values of Morisita's index greater than one indicate an aggregated dispersion, as assessed by an F statistic (Poole, 1974).

#### MUSSEL GROWTH AND AGE DISTRIBUTIONS

We used a slow speed, diamond bladed saw to section mussel shells to determine mussel ages by counting annuli on fresh dead shell (Neves and Moyer, 1988; Haag and Commens-Carson, 2008). Haag and Commens-Carson (2008) and Rypel *et al.* (2008) presented convincing evidence that mussels lay down annual growth lines. Mussel shells were first sectioned through the umbo and epoxied to a microscope slide or plexiglass plate, depending on size. The shell was then re-sectioned to provide a thin section and was sanded with fine sand paper (320–1500 grit), and then annuli were counted under a dissection microscope by two different technicians and averaged to estimate age. We were careful to use only specimens with intact, unweathered umbos so the first growth line would represent an age of 1 y.

We used the von Bertalanffy growth function (VBGF),

$$L(t) = L_{\infty} \left( 1 - e^{-K(t-t_0)} \right),$$

to model the length to age relationship of the mussels (Haag and Rypel, 2011). The variables are *t* (time, year of age), *t*<sub>0</sub> (*t* zero, x-axis intercept) the hypothetical age at zero length, *L*<sub>∞</sub> (*L* infinity), the maximum length reached, and *K*, a growth rate constant with units of reciprocal time (*e.g.*, year<sup>−1</sup>). Age at maturity was estimated both from the point where a 45° tangent intersected the fit curve, because growth in unionids is rapid prior to sexual maturity and decreases abruptly thereafter (McMahon and Bogan, 2001; Haag and Rypel, 2011), and by the empirical relationship between age at maturity and growth rate constant (*K*) from the von Bertalanffy growth function,

$$\alpha = 0.69K^{-1.03}$$

as determined by Haag (2012). In almost all cases (*see results*), both methods gave similar estimates. The VBGF curve's *t*<sub>0</sub> is hypothetical, and the age at a shell length of zero can be

negative (Haag and Rypel, 2011) which is biologically unreasonable. We therefore set  $t_0$  to zero to force the estimated growth curve to pass through the origin.

The resulting growth curves are presented for Inflated Heelsplitters ( $n = 76$ ) and the related Bluefers ( $n = 71$ ) and Fragile Paper Shells ( $n = 68$ ). In *P. purpuratus* obvious sexual dimorphism occurs in shell shape, and we were able to construct an age curve for both males and females, since females have a truncated posterior portion of the shell because of brooding glochidia. However, neither Inflated Heelsplitters nor Fragile Paper Shells have shell morphologies that are obviously sexually dimorphic.

*Fish assemblage sampling.*—To determine the relative abundance of the Freshwater Drum, we divided the range of the Inflated Heelsplitter in the Amite River into an upper, middle, and lower stretch and electro-fished each section in Spring, Summer, and Fall 2011, since the Inflated Heelsplitter is a long term brooder. Each site was electro-fished with a DC electrofishing boat, sampling a 700 m to 1 km stretch on each side of the river, as well as thalweg stretches, for 1200–1600s (Perret *et al.*, 2010). Three sites were sampled in the upper section and five each in the middle and lower section at each date. All fish were identified and returned to the river. Data for all 2419 fishes collected, at all three sampling dates and sites, were pooled and an importance curve generated for all fishes. To assess the relationship between the abundance of potential host fish and mussel abundance, we first calculated an average importance value for all fish hosts for each mussel species that had been verified by laboratory exposure experiments. Data on host fish use were taken from Williams *et al.* (2008) and Watters (2009) [http://www.biosci.ohio-state.edu/~molluscs/OSUM2/terms\\_hosts2.html](http://www.biosci.ohio-state.edu/~molluscs/OSUM2/terms_hosts2.html) and references therein. We then regressed average mussel density from our samples against these values. To be conservative, we only included fish hosts that were validated as producing large numbers of metamorphosed juvenile mussels in the laboratory trials and not just listed as hosts from anecdotal occurrence of glochidia on fish in the field.

## RESULTS

### DENSITY

Inflated Heelsplitters have a small range in the Amite River, stretching from the confluence of Spiller's Creek to Port Vincent on the Amite River (Fig. 1). The size of the circles indicates the total number of Inflated Heelsplitters collected at a site in 2007 (Brown *et al.*, 2010) and in this study. Sites without Inflated Heelsplitters are also noted. Inflated Heelsplitter abundance is greater in the lower part of its range, where disturbances from gravel mining or urbanization are less pronounced (see Fig. 1 inset and Brown *et al.*, 2010). The density of Inflated Heelsplitters was intermediate when compared to the other species (see *a posteriori* ranges in Table 1). *Quadrula refulgens*, *Plectomerus dombeyanus*, and *Potamilus purpuratus* were fairly abundant with densities above 0.25 per  $m^2$ ; and *P. inflatus* belonged to a large group of species with intermediate densities ranging from 0.234 to 0.05  $m^{-2}$ . Most of the abundant species, and species with intermediate abundances, had values of Morisita's index indicating aggregated dispersions (Table 1), including *P. inflatus*, and the dispersion pattern of *P. purpuratus* was fairly similar to its congener. In the case of the Inflated Heelsplitter, the samples with the five highest densities all came from one site, a shallow sand riffle protected by some large snags that mediated current flow.

### LIFE HISTORY

*Potamilus inflatus* matured after 1 y (both methods) and lived to be 7 to 8 y of age (Fig. 2A). Of the three species, it had the largest growth constant,  $K$ , of 0.69 and reached an

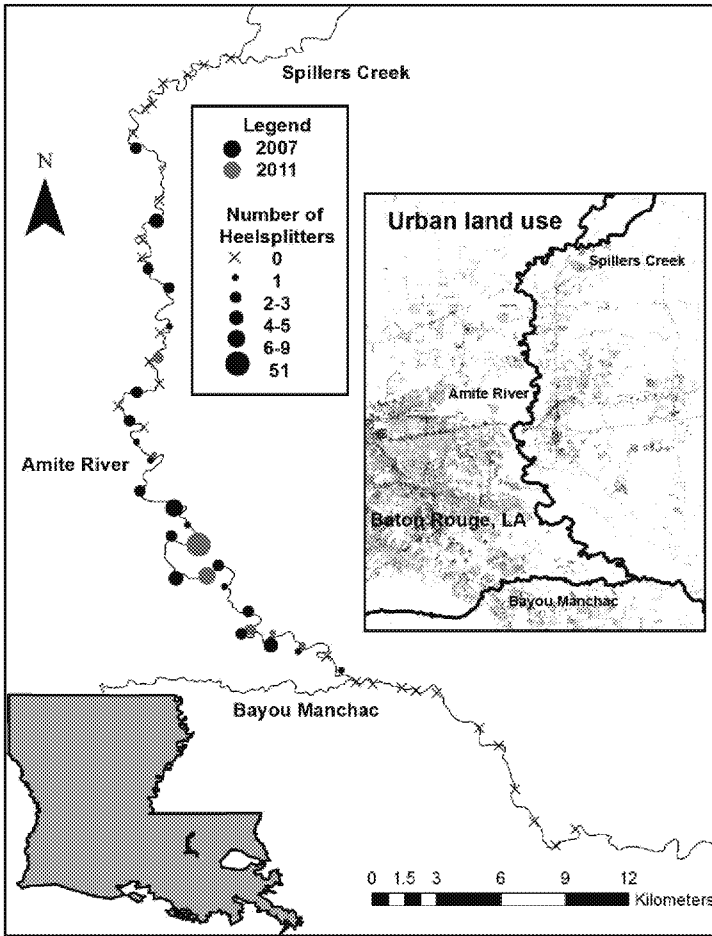


FIG. 1.—The range of the Inflated Heelsplitter, *Potamilus inflatus*, in the Amite River in Louisiana. Size of circles reflects numbers of Inflated Heelsplitters collected during 90 min of qualitative sampling (2007) or quantitative sampling (2011). Sites marked x had no Inflated Heelsplitters. Inset shows area covered by residential development. Gravel mining disturbances stop at Spiller's creek

asymptotic size of 113 mm shell length. *Leptodea fragilis* had a very similar life history (Fig. 2B), maturing at 1.5 y of age (both methods), dying after an age of 6 y and reaching an asymptotic size of 134 mm. *Potamilus purpuratus* had the most divergent life history of the three related species, with the lowest growth ( $K = 0.257$  for males and  $0.456$  for females), latest maturity [3 y for males (both methods) and 1.6 y for females, based on Haag (2012)] and largest asymptotic size, 204 mm shell length, after a life span of 30 y. Sexual dimorphism was fairly clear in *P. purpuratus* (Fig. 3) with males reaching larger sizes than females. Using the growth curve for Inflated Heelsplitters, we converted shell length histograms to estimate the age distribution (Fig. 4). Young recently mature Inflated Heelsplitters were quite common, suggesting the mussel is recruiting fairly well.

TABLE 1.—Densities of unionid mussels in the Amite River, from most to least abundant. Tukey's ranges are from a log-transformed one way ANOVA of densities

Species	Density/M <sup>2</sup>	Tukey's range	I <sub>δ</sub> <sup>1</sup>	F <sup>2</sup>
<i>Quadrula refulgens</i>	0.680	A	11.75	11.5**
<i>Plectomerus dombeyanus</i>	0.296	B	3.78	16.0**
<i>Potamilus purpuratus</i>	0.250	BC	4.33	9.25**
<i>Lampsilis teres</i>	0.234	BCD	6.91	14.7**
<i>Amblema plicata</i>	0.181	BCDE	6.49	10.8**
<i>Potamilus inflatus</i>	0.110	BCDE	8.16	8.8**
<i>Obliquaria reflexa</i>	0.092	BCDE	4.16	3.8*
<i>Glebulula rotundata</i>	0.082	BCDE	10.23	8.4**
<i>Lampsilis claibornensis</i>	0.048	CDE	2.76	1.79
<i>Leptodea fragilis</i>	0.043	DE	8.23	3.96*
<i>Villosa lienosa</i>	0.035	DE	4.27	2.1
<i>Quadrula nobilis</i>	0.029	DE	11.2	3.7*
<i>Pyganodon grandis</i>	0.027	DE	4.27	1.8
<i>Lampsilis ornata</i>	0.011	E	0.00	0.9
<i>Quadrula verrucosa</i>	0.005	E	18.67	1.6

<sup>1</sup> Morisita's index

<sup>2</sup> F test of significance of Morisita's index. One asterisk indicates P < 0.05, two P < 0.01

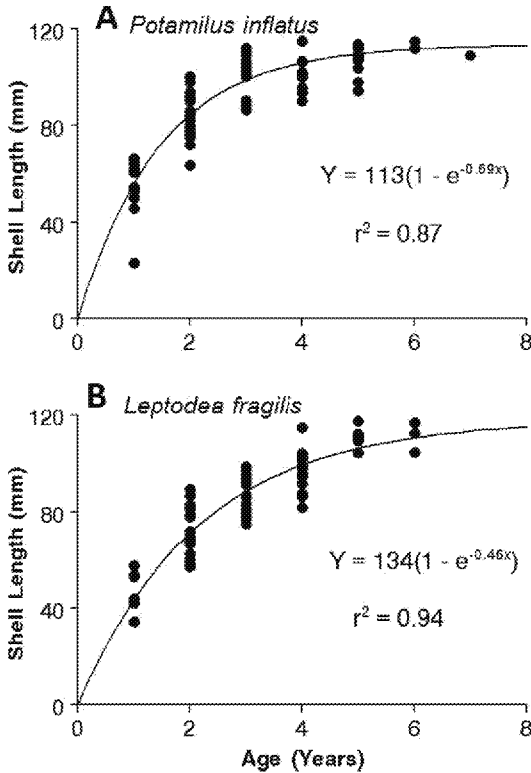


FIG. 2.—Shell length vs. age curves for the Inflated Heepsitter (A), and its close relative, the Fragile Paper Shell *Leptodea fragilis* (B). Equations are from a fit of a Von Bertalanffy function to the data



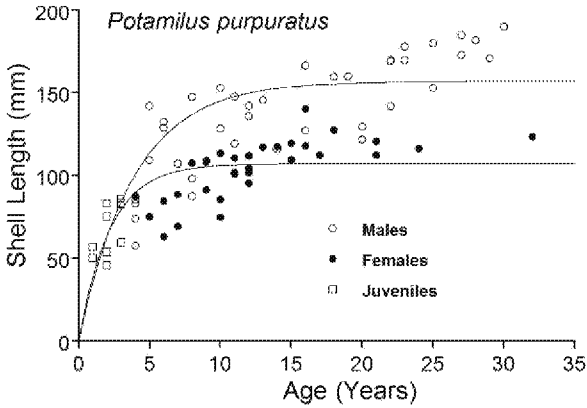


FIG. 3.—Shell length vs. age curves for the Bluefer, *Potamilus purpuratus*. Sexual dimorphism in growth between larger males and smaller females occurs in *P. purpuratus*. Individuals less than 3–4 y of age are juveniles. Growth curves are also plotted for both sexes

*Fish host.*—The fish assemblage in the Amite River contains at least 44 species (Table 2), and Freshwater Drums were intermediate in abundance (the 17th most abundant species). They were not sampled in the upper part of the Inflated Heelsplitter range but were sampled in the mid and lower sections of the Amite River. There was no clear relationship between mussel density and the average importance value for the known fish hosts for that mussel ( $F = 1.6$ ,  $P = 0.24$ , Fig. 5).

DISCUSSION

The Inflated Heelsplitter, *Potamilus inflatus*, has densities and a distribution similar to most unionid mussels in the Amite River and a clumped dispersion pattern common in unionids (Vaughn, 1997). However, it does have an extremely small range, approximately 20 km north and south of the Interstate Highway 10 bridge over the Amite River. Small

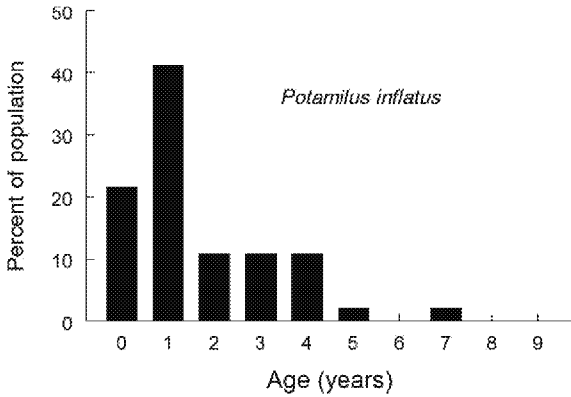


FIG. 4.—The age distribution of the Inflated Heelsplitter, *Potamilus inflatus*, in the Amite River. Size distributions were converted to an age distribution with the model in Fig. 2. Individuals labeled as “0” were less than 1 y of age

TABLE 2.—Relative importance values for the fish assemblage of sections of the Amite River inhabited by the Inflated Heelsplitter. Mussels considered from the literature to use the fish as a glochidial host are also indicated

Fish species	Relative importance	Mussels potentially hosted
<i>Cyprinella venustus</i>	1.000	
<i>Mugil cephalus</i>	0.907	
<i>Dorosoma cepedianum</i>	0.687	<i>P. grandis</i>
<i>Lepomis megalotis</i>	0.592	<i>V. lienosa</i> , <i>P. grandis</i> ,
<i>Lepomis macrochirus</i>	0.575	<i>A. plicata</i> , <i>G. rotundata</i> , <i>L. claibornensis</i> , <i>V. lienosa</i> , <i>Q. nobilis</i> , <i>P. grandis</i>
<i>Micropterus salmoides</i>	0.367	<i>A. plicata</i> , <i>L. claibornensis</i> , <i>V. lienosa</i> , <i>Q. nobilis</i> , <i>P. grandis</i> , <i>L. ornata</i>
<i>Lepomis microlophus</i>	0.162	
<i>Micropterus punctulatus</i>	0.134	
<i>Ictalurus furcatus</i>	0.125	
<i>Dorosoma petenense</i>	0.078	
<i>Lepisosteus oculatus</i>	0.071	<i>G. rotundata</i>
<i>Lepisosteus osseus</i>	0.065	<i>L. teres</i>
<i>Ictiobus bubalus</i>	0.048	
<i>Labidesthes sicculus</i>	0.043	<i>P. grandis</i>
<i>Ictiobus cyprinellus</i>	0.041	
<i>Moxostoma poeciliurum</i>	0.041	
<i>Aplodinotus grunniens</i>	0.032	<i>P. purpuratus</i> , <i>A. plicata</i> , <i>P. inflatus</i> , <i>L. fragilis</i> , <i>P. grandis</i> ,
<i>Fundulus olivaceus</i>	0.032	
<i>Ictalurus punctatus</i>	0.030	<i>A. plicata</i> , <i>V. lienosa</i> , <i>Q. nobilis</i> ,
<i>Pomoxis nigromaculatus</i>	0.030	<i>A. plicata</i> , <i>Q. nobilis</i> , <i>P. grandis</i>
<i>Pomoxis annularis</i>	0.024	<i>A. plicata</i> , <i>Q. nobilis</i> , <i>P. grandis</i>
<i>Pylodictis olivaris</i>	0.019	<i>Q. refulgens</i> , <i>A. plicata</i> , <i>Q. nobilis</i>
<i>Notropis atherinoides</i>	0.019	<i>A. plicata</i>
<i>Lepomis humilis</i>	0.015	<i>V. lienosa</i> , <i>P. grandis</i>
<i>Carpiodes carpio</i>	0.013	<i>P. grandis</i>
<i>Lepomis gulosus</i>	0.006	<i>A. plicata</i> , <i>P. grandis</i>
<i>Notemigonus crysoleucas</i>	0.006	<i>P. grandis</i>
<i>Trinectes maculatus</i>	0.006	<i>G. rotundata</i>
<i>Minytrema melanops</i>	0.006	
<i>Morone chrysops</i>	0.004	<i>A. plicata</i> , <i>G. rotundata</i> , <i>P. grandis</i>
<i>Lepomis cyanellus</i>	0.004	<i>A. plicata</i> , <i>G. rotundata</i> , <i>V. lienosa</i> , <i>Q. nobilis</i> , <i>P. grandis</i>
<i>Lepomis gibbosus</i>	0.004	
<i>Gambusia affinis</i>	0.004	<i>L. claibornensis</i>
<i>Pimephales vigilax</i>	0.004	
<i>Anguilla rostrata</i>	0.002	
<i>Ictiobus sp.</i>	0.002	
<i>Aneides natalis</i>	0.002	<i>Q. nobilis</i> , <i>P. grandis</i>
<i>Ichthyomyzon sp.</i>	0.002	
<i>Strongylura marina</i>	0.002	
<i>Percina caprodes</i>	0.002	
<i>Aphredoderus sayanus</i>	0.002	
<i>Cyprinus carpio</i>	0.0021	
<i>Morone mississippiensis</i>	0.0021	
<i>Opsopoeodus emiliae</i>	0.0021	

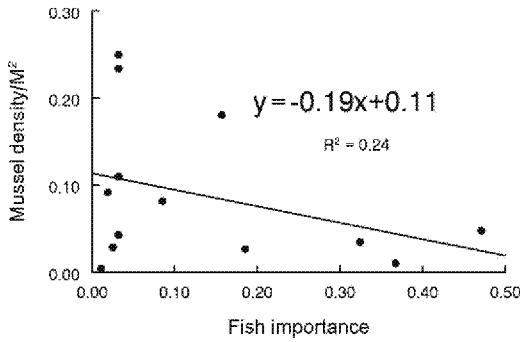


FIG. 5.—The relationship between host fish relative importance (increasing on the x axis) and mussel density. Host fish were determined from Williams *et al.* (2008) and other sources

ranges are a common characteristic of imperiled species (Gilpin and Soule, 1986). Inflated Heelsplitters do have what would be termed an “opportunistic” life history in comparison to many other unionids (Haag, 2012). For example, the average life span of eight other mussels in the Amite River (Daniel, 2012) is 24 y, with average age at maturity of about 3.6 y and an average growth constant of  $0.16^{-yr}$ . As might be expected with such a life history (Haag, 2012), the Inflated Heelsplitter age distribution is skewed towards younger individuals with one year olds quite common. Inflated Heelsplitters had the highest growth constant of the three species and a short life span. An inverse relationship was also reported between growth and life cycle length for unionids, as a group by Haag and Rypel (2011), possibly due to a negative tradeoff between energy available for early growth and longevity.

Life history variation can be arranged along a “fast to slow” continuum with fast species having relatively early maturity, fast growth, and short life cycles. Species with fast life cycles are usually considered to have greater mortality rates for adults (Charnov, 1991). Haag and Rypel (2011) found mussels in the tribes Anodontini and Lampsilini (to which *P. inflatus* belongs) to have the shortest life cycles and earliest maturity in unionids, although they also noted there was considerable variation within the lampsilids. Haag and Rypel (2011) and Haag (2012) also suggested opportunists had higher reproductive rates than species with periodic or equilibrium life histories. Vaughn (2012) found, in a long term comparative study of Oklahoma unionid populations, that mussels with longer brooding periods were more likely to go extinct; so the extended brooding interval of Inflated Heelsplitters may put them at risk. The sexual dimorphism in growth seen in *P. purpuratus*, which may also occur in *P. inflatus* (Hartfield and Garner, 1995; Williams *et al.*, 2008) is interesting. Haag and Rypel (2011) also found the same sexual dimorphism (males growing faster) in Mississippi populations of Bluefers. Although slower growth rates in females may simply be due to higher costs of producing and brooding glochidia, smaller females might also be more easily consumed by molluscivorous Freshwater Drum, possibly suggesting an unusual “suicidal” glochidial dispersal strategy (Haag, 2012).

As predicted by Vaughn (2012), the relatively low density of the host fish, the Freshwater Drum, may explain why Inflated Heelsplitters are at risk; although *Potamilius purpuratus* shares the same fish host and is one of the most common mussels in the river. There are no impoundments in the lower Amite River as it flows through Louisiana to interrupt fish movement, but Freshwater Drum were still not found in the upper part of the Inflated Heelsplitter’s range, although drum do move large distances (see Vaughn, 2012). There

appeared to be little obvious relationship on the whole between the average importance value of fish hosts and the density of the mussel species sampled here. However, as Haag (2012) points out, correlating mussel and host fish distributions or abundances can be problematic; since not all host fish have been determined, surveys of fish abundance can be biased (especially in the case of Freshwater Drum that are often found in deeper harder to sample pools) and both mussel and host fish distributions may have been altered anthropomorphically. However, the data suggest at least there is no strong easily observed positive relationship between mussel and host fish abundance. Other potential factors that may be important in limiting the distribution of Inflated Heelsplitters include gravel mining, which destabilizes the channel and increases chances that mussels will be stranded by low water (Hartfield, 1993) reducing the abundances of Inflated Heelsplitters and other unionids in the upper portion of the Amite River in Louisiana (Brown and Curole, 1997). Urbanization of the watershed in the lower portion of the Amite River has also increased the frequency and magnitude of flooding events in the Amite River (Xu and Wu, 2006), and Inflated Heelsplitter abundance was found to be negatively correlated with human alteration of the riparian zone (Brown *et al.*, 2010).

In summary, this endangered mussel does have a small range in the Amite River but has densities within that range similar to most other unionids and a similar dispersion pattern. Inflated Heelsplitters have, as predicted (Haag, 2012), an opportunistic life history strategy with more rapid growth, earlier maturity, and shorter life cycles than most of the other unionids, which Haag (2012) considered an adaptive set of traits for dealing with frequent disturbances and rebounding from small population sizes. Its relatively rare host fish may limit the distribution of the mussel, although channel alteration from upstream gravel mining or high shear stresses during spates common in urbanized stretches of the river may also be important. Conservation of this species in Louisiana may therefore require more attention to conserving surrounding riparian woodlands (Brown *et al.*, 2010).

*Acknowledgments.*—We thank Drs. William Kelso and Michael Kaller, and Raynie Bamberger Harlan (School of Renewable Natural Resources, Louisiana State University) for assistance in sampling the Amite River fish assemblages. The State Wildlife Grant Program (Grant T 61) of the Louisiana Department of Wildlife and Fisheries and a Louisiana EPSCoR Pfund grant provided funding for this project. Dr. Wendell Haag kindly instructed us in shell preparation and age determination. We thank Dr. Barry Aronhime, Laura Brown, Jonathan McNair, and Luke Gibson for help with field work.

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SUBMITTED 10 JUNE 2013

ACCEPTED 21 DECEMBER 2013